

## Behavioral Thermoregulation in a Sexually and Developmentally Dichromatic Neotropical Primate, the Black-and-Gold Howling Monkey (*Alouatta caraya*)

JÚLIO CÉSAR BICCA-MARQUES<sup>1,2\*</sup>

AND CLÁUDIA CALEGARO-MARQUES<sup>2</sup>

<sup>1</sup>Department of Anthropology, University of Illinois,  
Urbana, Illinois, 61801

<sup>2</sup>University of Illinois, Urbana, Illinois 61801

**KEY WORDS** heat balance; coat color; size; age; resting; positional behavior; sexual selection

**ABSTRACT** Behavioral thermoregulation in primates may provide a means for the conservation of heat during periods of low ambient temperature and/or food shortage as well as a way to dissipate heat under hot conditions. This article focuses on behavioral thermoregulation in a sexually dichromatic primate, the black-and-gold howling monkey (*Alouatta caraya*). Two models have been proposed to explain the evolution of sexual dichromatism in this species: thermoregulation and sexual selection. Five hypotheses associated with thermoregulatory behaviors are tested. These are as follows: (1) energy-conserving postures are used mainly under low ambient temperatures; (2) sunny resting places are selected during periods of low temperature; (3) exposure of the less-insulated ventral region to sunlight decreases with increasing temperature; (4) black-colored adult males use energy-conserving postures, sunny places, and exposure of the ventral region to sunlight less frequently than do blonde-colored adult females; and (5) smaller individuals use energy-conserving postures, sunny places, and exposure of the ventral region to sunlight in significantly greater frequency than do larger individuals. Over a 12-month period, behavioral data were collected on a free-ranging habituated group of 15–17 howlers of all age-sex classes. Ambient temperature was measured each hour. The results indicate that during resting, howlers showed a consistent use of heat-conserving postures, showed a preference for sunny places, and exposed their ventral region to sunlight under low ambient temperatures. A preference for shady places, heat-dissipating postures, and exposure of the back were observed under high ambient temperatures. Despite sex differences in adult color patterns and differences in size between age classes, no significant age or sex differences in thermoregulatory behaviors were detected. Failure to confirm a thermoregulation model implies that sexual selection may be responsible for sexual dichromatism in this species. *Am J Phys Anthropol* 106:533–546, 1998.

© 1998 Wiley-Liss, Inc.

*Alouatta caraya* (Atelidae, Alouattinae), the black-and-gold howling monkey (Rowe, 1996), is among a handful of primate species that exhibit sexual dichromatism (Crockett, 1987). In this species, adult males are black and adult females are blonde. A male's fur darkens gradually from blonde to black as

Contract grant sponsor: National Research Council-Brasil; contract grant number: 404457/88-6; Contract grant sponsor: World Wildlife Fund-US; contract grant number: 6573; Contract grant sponsor: Brazilian Government/CAPES; contract grant number: 1823/95-3.

\*Correspondence to: Júlio César Bicca-Marques, Department of Anthropology/UIUC, 109 Davenport Hall, Urbana, IL 61801. Tel: (217) 344-2904. Fax: (217) 244-3490. E-mail: jmarques@uiuc.edu

Received 10 March 1996; accepted 28 April 1998.

he matures. This may begin soon after the first months of life (4–6 months; Bicca-Marques, 1991). The rate of color change, however, seems to vary between populations (Bicca-Marques, 1989–1990). Black-and-gold howlers are also sexually dimorphic. Adult males are 47% heavier than adult females (Thorington et al., 1979).

Two models have been proposed to explain the evolution of sexual dichromatism in *A. caraya*. Thorington et al. (1979) have suggested that pelage color in *Alouatta* is related to solar insulation. Thus, the dichromatism observed in *A. caraya* could be related to the marked seasonal changes in temperature within its range and could reflect seasonal sex-based differences in energetic and thermal requirements—the thermoregulation model. Because the amount of visible light absorbed by the coat depends on its color—darker-colored forms absorb more incident energy than lighter-colored ones (Schmidt-Nielsen, 1990)—Thorington et al. (1979) suggested that the advantages of being an adult male or an adult female black-and-gold howler vary seasonally. In the cold season, a dark coat would favor heat gain through solar radiation. A blonde coat, on the other hand, would result in a lower heat gain during the hot season.

Crockett (1987), however, believes that the thermoregulation model “does not really address why sexual dichromatism evolved in the first place” (p. 118) and argues that this phenomenon in *Alouatta* may be involved in signalling sexual identity—the sexual selection model. She further believes that “female choice of distinctive males (epigamic selection) seems a more likely selective pressure than intrasexual competition for mates” (Crockett, 1987:118). According to her model, sexual dichromatism may have evolved through the selection of distinctive males (resulting from chance mutations) by females that emigrated from their natal groups.

In this study, we evaluate the thermoregulation model to explain the evolution of sexual dichromatism by assessing *A. caraya*'s behavioral thermoregulation. We also discuss the sexual selection model. Behavioral thermoregulation is a process of select-

ing particular body orientations and environmental sources of heat (Casey, 1981). Changes in positional behavior (Prost, 1965) modify the relationship between the animal and its surrounding environment. This affects energy exchange through radiation, conduction, convection, and evaporation (Paterson, 1986, 1994). Several primates have been observed using behavioral tactics to either conserve or dissipate heat (*A. caraya*—Zunino, 1986; *A. palliata*—Chivers, 1969; Milton et al., 1979; Paterson, 1980, 1981, 1986; Young, 1982; *Aotus trivirgatus*—LeMaho et al., 1981; *Colobus guereza*—Oates, 1977; *Colobus polykomos*—Dasilva, 1993; *Macaca arctoides*—Dahl and Smith, 1982; *Macaca fuscata*—Paterson, 1994; *Macaca mulatta*—Dahl et al., 1982; *Papio cynocephalus*—Stelzner and Hausfater, 1986; *Lemur catta*—Jacobson and Nash, 1995).

Five hypotheses are tested concerning the use of thermoregulatory behaviors during rest by *A. caraya* under changing ambient temperatures.

Hypothesis 1: postural behavior varies according to ambient temperature. Energy-conserving postures, which promote small surface-volume ratios, will decrease in frequency, and energy-dissipating postures will increase with increasing air temperature.

Hypothesis 2: microhabitat selection is related to ambient temperature. Sunny resting places will be selected during periods of low temperature to gain heat from solar radiation, whereas shady places will be increasingly preferred at high ambient temperatures.

Hypothesis 3: those regions of the body howlers expose to sunlight vary according to ambient temperature. The coat of the ventral region is less insulated than that of the dorsal region (Paterson, 1981). Thus, its exposure to sunlight will decrease and the exposure of the dorsal region will increase with increasing temperature.

Support or rejection of these first three hypotheses provides the basis for evaluating the final two hypotheses.

Hypothesis 4: due to the potential consequences of color and size differences regarding heat balance, adult males and females adopt different thermoregulatory strategies.

Adult males will use energy-conserving postures, sunny places, and the exposure of the ventral region to sunlight at a lesser extent than will adult females. This hypothesis assumes minimal sex differences in morphological traits other than coat color and body size.

Hypothesis 5: age classes differ in their use of positional thermoregulatory behaviors. According to Heatwole (1983), smaller individuals (infants and juveniles) tend to lose heat at a greater rate than do larger (older) animals. This is due to the larger surface-volume ratio of immature animals. Individuals of the smallest classes (infants and juveniles) will use energy-conserving postures, sunny resting places, and the exposure of the ventral region to sunlight significantly more than larger-bodied individuals. Larger monkeys will initiate heat-dissipating behaviors at lower temperature levels.

#### MATERIALS AND METHODS

This study was conducted from August 1989 to July 1990 at Estância Casa Branca (29° 37' S, 59° 17' W, 100 m a.s.l.), Alegrete-RS, Brazil. This area represents the southern limit of *A. caraya*'s distribution (Bicca-Marques, 1990). *A. caraya* lives mainly in gallery and semideciduous forests (Santini, 1985) throughout eastern Bolivia, Paraguay, northern Argentina, and central-western and southern Brazil (Hill, 1962). The distribution of *Alouatta fusca clamitans*, the only other sexually dichromatic howling monkey, also extends to 30° S latitude (Prates et al., 1993).

The study area is a 2 ha seminatural forest characterized by a mixture of native and exotic plant species (Bicca-Marques, 1990). A detailed description of the study site has been published elsewhere (Bicca-Marques, 1991). The region has a subtropical climate (Cfa type of Koeppen's classification) with distinct seasons (summer, fall, winter, and spring) (Moreno, 1961). Climatic data collected from 1931 to 1974 at the Meteorological Station of Alegrete (29° 46' 47" S, 55° 47' 15" W; 100 m a.s.l.) indicate an annual mean rainfall of 1,532 mm and an annual mean air temperature of 18.6°C (Fig. 1). Monthly mean air temperature ranges from 13.1°C (July) to 24.9°C (January). Mini-

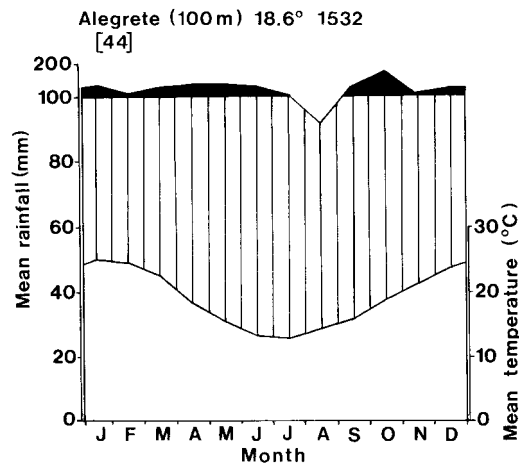


Fig. 1. Climate diagram (see Walter, 1971) of the Municipality of Alegrete near to the study site. Data for Meteorological Station of Alegrete, monthly averages 1931–1974. Elevation = 100 m; mean annual temperature = 18.6°C; mean annual rainfall = 1532 mm; number of years of meteorological data collection = 44.

um and maximum monthly mean temperature ranges between 8.8°C and 31.4°C. The absolute minimum and maximum temperatures were –4.1°C and 40.4°C, respectively. The annual mean relative humidity is approximately 75%, with monthly means ranging from 66% (December) to 84% (July) (Brasil-IPAGRO, 1989).

The size of the study group ranged from 15 to 17 individuals. In August 1989 the group was composed of 5 adults (1 male:4 females), 2 subadults (1:1), 7 juveniles (2:5), and 3 infants (2:1). Changes in group composition were recorded by Calegare-Marques and Bicca-Marques (1996). These age classes differed in average body weight: infants (0.7 kg), juveniles (2.3 kg), subadults (3.9 kg), adult females (4.4 kg), and adult males (6.7 kg) (Malinow et al., 1966; Pope, 1966; Thorington et al., 1984; Rumiz, 1985).

Behavioral data were collected from dawn until dusk for a total of 60 days (5 days per month) throughout the year (here, January–March = summer, April–June = fall, July–September = winter, and October–December = spring). Five-minute instantaneous scan samples (Altmann, 1974) were conducted every 15 minutes. A total of 2,980 scan samples distributed across 745 hours of observation were collected. A mean of 12.7

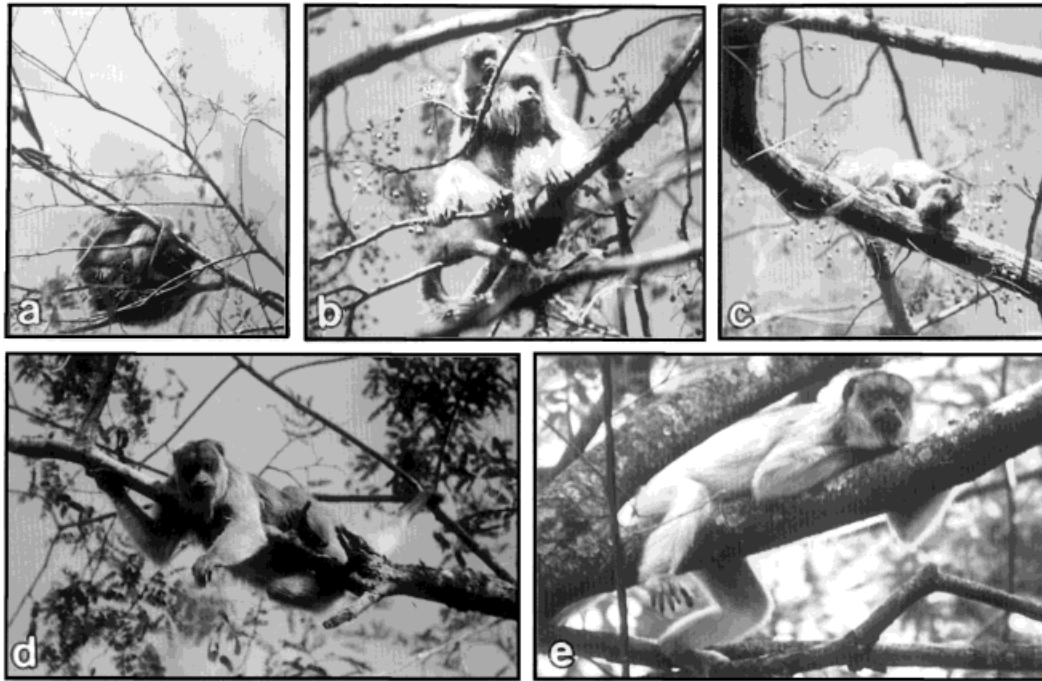


Fig. 2. Body postures used by black-and-gold howling monkeys during resting. (a) Curled, (b) sitting, (c) lying, (d) spread, and (e) stretched. Although the right arm of the female in (e) is flexed, it is not leaned against the body and the left arm is extended; this posture is better described as stretched.

individuals were observed in each sample. No observations were made on rainy days.

During monkey resting, the following data were recorded: (1) body posture, (2) presence or absence of direct sunlight based on the cloudiness of the sky and the presence of shade, (3) resting place (sunny or shady), (4) presence or absence of wind, and (5) the main body portion (dorsal, ventral, or lateral) exposed to sunshine when an animal was resting in a sunny place. Records of infants resting while clinging to their mothers' ventrum were excluded from the analysis. This was done to include only data across comparable age classes. Because no data were recorded on the use of wind-protected or wind-exposed resting places, the qualitative wind data collected were not analyzed.

Resting postures were divided into five categories: (1) curled—arms and legs are kept flexed and close to the body while the back is bent and the head is near the tail, giving the body a spherical shape in which

the ventrum is completely hidden; (2) sitting—animal in sitting position with legs flexed, back slightly curved, and ventrum partially exposed; (3) half extended (hereafter, lying)—animal lying with back extended and members (arms and legs) flexed and close to the body; (4) three quarters extended (spread)—animal lying with back extended and two members flexed and two extended; and (5) fully extended (stretched)—animal lying with back and all members extended (Fig. 2) as described by Paterson (1981, 1986). Huddling, a behavior in which three or more individuals rest leaning against one another, was qualitatively recorded. To relate the use of positional behaviors to ambient temperature, air temperature was measured each hour with a mercury thermometer placed at a height of 2 m in the shade. Hourly daytime ambient temperatures ranged from 5°C to 35°C.

To weight the changes in group composition, data were analyzed on a monthly basis



using the frequency method (Oates, 1977). The number of monthly records in which an age-sex class performed a particular behavior under a certain ambient temperature was divided by the number of individuals in that class in the month. These monthly data were grouped into 2°C-temperature classes (5–6°C, 7–8°C, and so on). The percentage of use of each behavior was then calculated for each temperature interval. To analyze the influence of ambient temperature on postural behavior during resting, a mean posture was calculated for each temperature class by giving a rank for each resting posture (curled = 1, sitting = 2, lying = 3, spread = 4, stretched = 5) and taking into account their frequencies of use. This mean posture, therefore, may vary from 1 (if only curled is used under a certain temperature class) to 5 (if only stretched is used). Relationships between ambient temperature and the use of each resting posture and the mean posture across all temperatures were analyzed by Pearson correlation coefficients in SYSTAT (Wilkinson, 1990). The similarity of the patterns observed among age-sex classes was tested by matrix correlation tests or normalized Mantel statistic  $Z(r)$  using the NTSYS program (Rohlf, 1994). Data points presented in Figure 3 and curves presented in Figures 4–6 were smoothed by the hanning method (Velleman and Hoaglin, 1981), where  $y_t = \frac{1}{4}y_{t-1} + \frac{1}{2}y_t + \frac{1}{4}y_{t+1}$ . Statistical tests, however, were performed using raw results.

## RESULTS

A total of 18,539 records of resting were collected. Sitting and curled were the most common postures, accounting for 38.2% and 22.8% of all records, respectively. Lying, spread, and stretched accounted for the remaining 39%.

### Postural behavior and ambient temperatures

The use of resting postures was influenced significantly by the thermal environment (Fig. 3) ( $r = 0.958$ ,  $n = 16$ ,  $P < 0.001$ ). Curled was heavily used at lower ambient temperatures ( $r = -0.960$ ,  $n = 16$ ,  $P < 0.001$ ). Whereas the use of curled was inversely related to the temperature, the use of spread

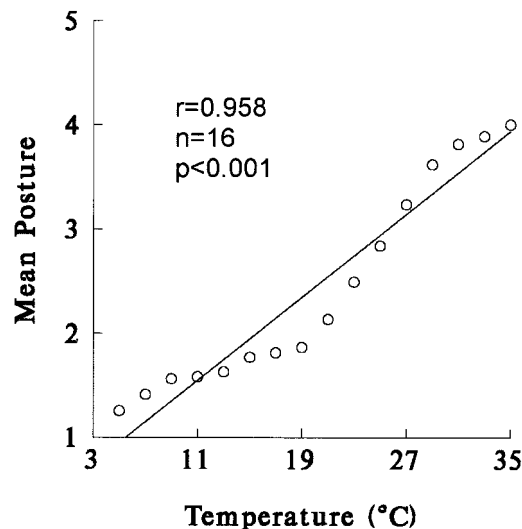


Fig. 3. Relationship between mean resting posture and ambient temperature in the shade (see Materials and Methods).

( $r = 0.914$ ,  $n = 16$ ,  $P < 0.001$ ) and stretched ( $r = 0.864$ ,  $n = 16$ ,  $P < 0.001$ ) was positively related to temperature. These latter postures were used most frequently during resting at higher ambient temperatures. Sitting and lying were mainly utilized in the middle of the air temperature range observed. Sitting tends to increase in use from 5°C to 21°C ( $r = 0.895$ ,  $n = 9$ ,  $P = 0.001$ ) and to decrease in use from 23°C to 35°C ( $r = -0.953$ ,  $n = 7$ ,  $P = 0.001$ ). The use of lying also tends to increase with increasing temperatures from 5°C to 23°C ( $r = 0.865$ ,  $n = 10$ ,  $P = 0.001$ ) and to decrease from 25°C to 35°C ( $r = -0.946$ ,  $n = 6$ ,  $P < 0.01$ ) (Fig. 4). These data support hypothesis 1, which indicates the use of energy-conservation postures with decreasing air temperature and the use of energy-dissipating postures with increasing air temperature.

### Microhabitat selection and ambient temperatures

The relationship between microhabitat selection and ambient temperature is shown in Figure 5. Under lower ambient temperatures, howlers rested in sunny places; under higher temperatures, they tended to avoid exposure to sunlight ( $r = -0.940$ ,  $n = 16$ ,  $P < 0.001$ ). These results support hypoth-

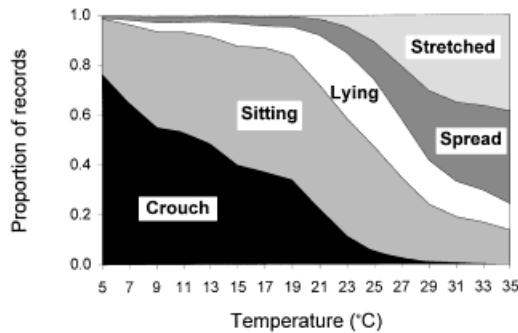


Fig. 4. Use of the resting postures by black-and-gold howling monkeys under changing ambient temperature. Curves were smoothed (see Materials and Methods).

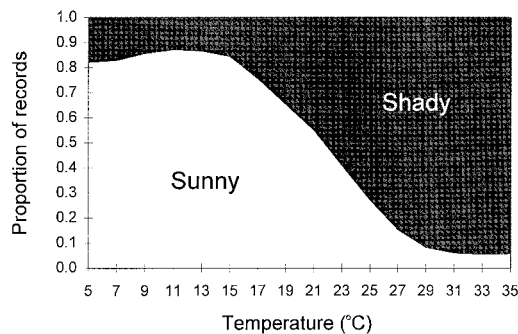


Fig. 5. Use of sunny and shady resting places by black-and-gold howling monkeys under changing ambient temperature, excluding records collected under cloudy conditions. Curves were smoothed (see Materials and Methods).

esis 2 and demonstrate a significant relationship between microhabitat use and ambient temperature.

#### Exposure of body regions to sunlight and ambient temperatures

The results indicate that ambient temperature had a significant influence on body orientation. When temperature was high, exposure of the ventral region was avoided ( $r = -.865$ ,  $n = 16$ ,  $P < 0.001$ ). However, because exposure of the lateral portion of the body to sunlight may also expose the ventral or dorsal regions, these data were reanalyzed. Using only those records when howlers exposed either the ventral or the dorsal region to sunlight, differences between body orientation in relation to temperature were also significant (dorsal exposure:  $r = 0.852$ ,

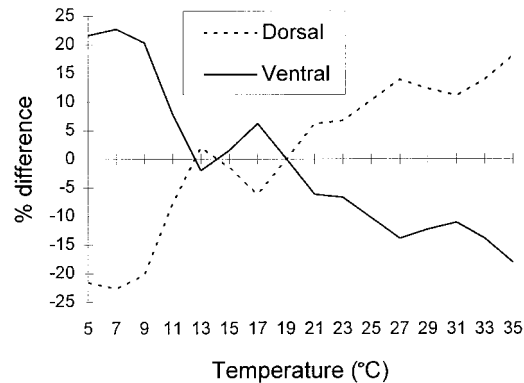


Fig. 6. Differences between the observed and expected percentages of exposure of the ventral and dorsal body regions to sunlight by black-and-gold howlers under changing air temperatures. Curves were smoothed (see Materials and Methods).

$n = 16$ ,  $P < 0.001$ ; ventral exposure:  $r = -0.852$ ,  $n = 16$ ,  $P < 0.001$ ). Figure 6 shows the difference between the observed and expected (assuming equal orientations) percentages of exposure to sunlight of both regions according to the air temperature. The ventral region of the body was more exposed than expected only under lower temperatures. This region appears to have a less dense coat and may be less well insulated. On those few occasions when howlers rested in sunny places under hotter conditions, they exposed mainly the dorsal region. Hypothesis 3 is accepted, indicating that it is likely that body orientation plays an important role in thermoregulatory behavior.

#### Sexual dimorphism and thermoregulatory behaviors

Given an overall set of relationships among ambient temperature, sunlight, body orientation, positional behavior, and thermoregulation, evidence of whether coat color affected these relationships was examined. Despite differences in color and body size, choice of microhabitat and exposure of body regions to sunlight did not differ between adult males and adult females when resting (Matrix correlation:  $r = 0.76$  and  $r = 0.99$ , respectively;  $P < 0.01$ ). Certain trends, however, were detected along limited temperature ranges. The adult male utilized shady resting places more frequently than did adult

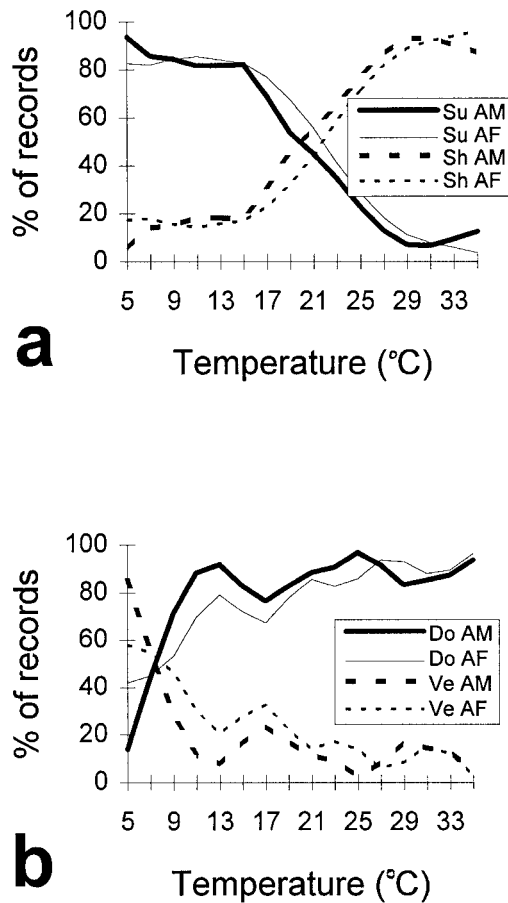


Fig. 7. (a) Percentage of records utilizing sunny (Su) and shady (Sh) resting places, and (b) Percentage of sunny records (excluding records of the lateral region) exposing the ventral (Ve) and dorsal (Do) region of the body to sunlight by adult male (AM) and adult female (AF) classes of black-and-gold howlers under changing air temperatures.

females under higher air temperatures (17–31°C) (Fig. 7a). The adult male also exposed his dorsal region to sunlight more frequently than did the adult female under lower air temperatures (7–25°C) (Fig. 7b). Outside this subset of temperature ranges, no consistent patterns were detected. For example, at temperatures below 17°C, there were no consistent differences in male/female microhabitat selection (Fig. 7a). These results do not support the contention that differences in color or size between males and females serve a clear thermoregulatory function. Hypothesis 4 is rejected.

#### Age variation in thermoregulatory behaviors

Irrespective of sex, matrix comparisons among adult, juvenile, and infant age categories indicated no significant differences in the use of resting postures. Subadults differed slightly from all other classes (Table 1); however, their overall pattern was consistent with other group members (Table 2). Due to the high degree of similarity between all other classes, patterns found in subadults cannot be attributed to differences in body size.

In relation to microhabitat selection and the exposure of body regions to sunlight, matrix comparisons also failed to show differences consistent with the predictions of hypothesis 5 (Table 1). Infants showed a weak tendency toward higher exposure of the dorsal region to sunlight. Despite substantial differences in the surface-volume ratio between age/size classes, the data do not support the contention that body size had a significant effect on the use of thermoregulatory behaviors in *A. caraya*.

#### Interindividual spacing

Changes in interindividual distance also appear to be a part of thermoregulatory behavior. Ad libitum observations indicate that during periods of low ambient temperature, infants spend a considerable amount of their resting time clinging to their mothers' ventrum. Under colder conditions, several individuals—not just infants and their mothers—rested together. During the colder temperatures of the morning and end of the afternoon, especially in the winter, all 17 members of the group rested in a single cluster (Fig. 8a). In such clusters, larger individuals seemed to occupy peripheral positions, while younger ones rested in the middle. This structural configuration may aid smaller individuals in avoiding excessive amount of heat loss to the cold environment.

By contrast, an increase in temperature resulted in an increase in interindividual distance (Fig. 8b). Qualitative observations offer evidence that resting in close proximity to the black adult male was actively avoided during periods of high temperatures. During

TABLE 1. Matrix correlation coefficients<sup>1</sup> of similarity (*r*) and probability levels (*P*) for each comparison among age classes of black howlers in terms of postural behavior and microhabitat selection/body regions exposed to sunlight

	Postural behavior			
	Adults	Subadults	Juveniles	Infants
Microhabitat selection/body region exposed to sunlight				
Adults	—	<i>r</i> = 0.70 <i>P</i> < 0.01	<i>r</i> = 0.99 <i>P</i> < 0.01	<i>r</i> = 0.99 <i>P</i> < 0.01
Subadults	<i>r</i> = 0.22 <i>P</i> < 0.05	—	<i>r</i> = 0.74 <i>P</i> < 0.01	<i>r</i> = 0.70 <i>P</i> < 0.01
Juveniles	<i>r</i> = 0.60 <i>P</i> < 0.01	<i>r</i> = 0.85 <i>P</i> < 0.01	—	<i>r</i> = 0.99 <i>P</i> < 0.01
Infants	<i>r</i> = 0.74 <i>P</i> < 0.01	<i>r</i> = 0.70 <i>P</i> < 0.01	<i>r</i> = 0.88 <i>P</i> < 0.01	—

<sup>1</sup> Data used in the matrix comparisons in terms of postural behavior are presented in Table 2. Probability levels defined according to Lapointe and Legendre (1992).

TABLE 2. Percentage of use of resting postures by age classes of *A. caraya* under changing ambient temperature

Temperature (°C)	Curled				Sitting				Lying				Spread				Stretched			
	Ad	Sb	Jv	In	Ad	Sb	Jv	In	Ad	Sb	Jv	In	Ad	Sb	Jv	In	Ad	Sb	Jv	In
5–6	75	97	82	78	24	3	18	22	0	0	0	0	1	0	0	0	0	0	0	0
7–8	64	70	61	53	31	29	35	47	2	1	2	0	3	0	2	0	1	0	0	0
9–10	52	53	52	51	41	41	39	42	4	2	7	7	2	3	2	1	1	0	1	0
11–12	53	49	54	53	40	45	38	40	4	2	4	5	3	3	3	1	0	1	1	1
13–14	54	57	53	50	40	40	42	43	4	2	3	6	2	0	1	0	0	0	0	1
15–16	32	39	30	34	53	44	50	53	11	14	16	12	3	2	3	0	0	0	0	1
17–18	35	39	41	40	50	52	50	55	9	3	4	4	5	5	4	0	1	1	1	1
19–20	38	37	40	38	48	52	48	54	9	8	9	7	4	2	3	1	0	0	1	0
21–22	21	23	21	16	51	51	48	61	20	20	25	21	8	4	4	3	0	2	1	0
23–24	9	13	11	8	47	47	41	55	24	27	35	29	13	10	10	6	7	3	3	3
25–26	5	6	4	4	43	41	42	56	24	22	35	33	16	20	13	6	11	11	7	2
27–28	2	4	3	3	35	25	29	35	21	20	25	39	22	27	21	13	20	25	23	10
29–30	1	1	0	0	22	20	17	34	16	13	15	27	31	32	30	21	31	35	38	18
31–32	1	0	1	0	17	17	14	22	13	12	13	17	39	32	29	31	30	39	43	30
33–34	0	0	0	0	18	19	18	25	14	10	16	21	36	33	33	18	32	38	33	36
35	0	0	0	0	15	13	9	10	9	5	3	28	45	43	36	30	32	39	53	33
Average	28	30	28	27	36	34	34	41	12	10	13	16	15	14	12	8	10	12	13	8

Ad, adults; Sb, subadults; Jv, juveniles; In, infants.

cold periods, however, the adult male seemed to be preferred as a resting partner. These patterns suggest that males store more heat than females. Such expectations, however, require rigorous tests using quantitative data. Moreover, during periods of high ambient temperatures, howlers periodically moved short distances within the same tree. As suggested by Paterson (1981), this behavior may occur so that a resting place in a colder region of the tree may be found.

## DISCUSSION

### Behavioral thermoregulation

Based on data collected on a group of wild mantled howling monkeys (*A. palliata*), there was evidence that individuals used postural behaviors to regulate body temperature. Postural adjustments change the body surface

area to volume ratio, and this affects the radiational, convective, and conductive heat-exchange properties of the animal and its surrounding environment (Paterson, 1981). In this study, curled (which reduces body surface area to volume ratio) was used as an energy-conserving posture. A smaller surface-volume ratio may decrease the animals' loss of heat in a colder environment. Conversely, spread and stretched postures function to dissipate heat. According to Schmidt-Nielsen (1990), naked or poorly furred areas can more easily change heat with the environment than heavily furred and more insulated areas. Thus, in the latter postures, the increased contact between howlers' hands, feet, face, and naked portion of the tail with the environment may play an important role in heat dissipation through conduction dur-





Fig. 8. (a) Cluster of individuals used during resting under low ambient temperatures. (b) Individual resting by black-and-gold howling monkeys during hot periods.

ing hotter periods. Moreover, the gain of energy from sunshine during cold periods and the increased heat loss, or at least the avoidance of solar energy gain by resting in shady places during hot periods, seem to be important elements of the howlers' thermoregulatory behavior.

Support for the first three hypotheses indicate the importance of behavioral thermoregulation in black-and-gold howlers. Under low ambient temperatures, they tend to rest using the curled posture in sunny places to conserve body heat while gaining heat from sunlight. In this way, the price of endothermy can be behaviorally minimized by taking advantage of solar radiation (Morse, 1980; Schmidt-Nielsen, 1990). Young (1982) cited the competition between turkey vultures (*Cathartes aura*) and howling monkeys (*A. palliata*) for early-morning sunning canopy places in emergent trees as an important source of solar heat. In addition, Bicca-

Marques (1993) found that in *A. caraya* during the winter—the most stressful season in terms of ambient temperature—the amount of time devoted to resting was inversely related to the ambient temperature. In comparison, under conditions of high ambient temperatures howlers spread and stretched in shady places. When resting in sunny places during the latter periods, however, they avoided exposure of the less-insulated ventral region to sunlight.

An additional way to conserve heat during cold periods may be achieved through the behavior called huddling or clustering (see Canals et al., 1989; Roverud and Chappell, 1991; Stapp et al., 1991; Yahav and Buffenstein, 1991). According to Paterson (1986: 236), huddling results in “an effective change of shape and a direct modification of the microhabitat surrounding the individual.” This behavior seems to be particularly important to infants, as was described by Hull (1973).

According to Dasilva (1993) and Young (1982), thermoregulatory behaviors seem to be particularly important to folivorous primates, whose energy-poor diet may impose the need for energy-conserving behaviors. This may be especially true during periods of food shortage and low ambient temperature (Montgomery and Sunquist, 1978; Young, 1982; Dasilva, 1993). Howlers are the most folivorous New World primates and include a relatively large quantity of mature leaves in their diet (see Neville et al., 1988). The howler group in this study had an annual diet composed of 34.4% mature leaves and 26.5% immature leaves and petioles (Bicca-Marques and Calegari-Marques, 1994a).

In addition to the use of particular positional behaviors, howling monkeys also utilize other behavioral patterns to conserve energy. The study subjects spent an average of 61.6% of the day resting. The amount of time spent resting increased during both the coldest periods in the winter and the hottest periods in the summer (Bicca-Marques, 1993). Howlers also use a slow deliberate mode of quadrupedalism—an energy-minimizing type of locomotion (Rosenberger and Strier, 1989). Quadrupedalism accounted for 68.9% of the locomotion records of the study

group (Bicca-Marques and Calegario-Marques, 1995).

Despite the striking sexual dimorphism observed among adult black-and-gold howlers, no consistent differences in thermoregulatory behaviors were detected between males and females. Changing seasonal advantages due to sexual dichromatism, as proposed by Thorington et al. (1979), were not supported in the present study. The only sex difference identified was the marginally greater use of shady resting places and back exposure to sunlight by the adult male, and this was evident only within a limited temperature range (11–25°C). The adult male did rest significantly more than the adult female throughout the year regardless of temperature conditions (Bicca-Marques and Calegario-Marques, 1994b). Other morphological traits, such as coat structure, insulation, hair optical quality, and skin color, may change heat balance (Walsberg et al., 1978; Parker, 1988; Walsberg, 1983, 1988a,b; Walsberg and Schmidt, 1989). Although both sexes have the same skin color, whether other pelage traits differ between the sexes is unknown. Even in the case of differences in one of these traits, coat color per se could not adequately explain possible seasonal advantages. This is because light coats can be thermally advantageous (losing less heat) over dark ones under windy, cold conditions. Depending on wind velocity, convective cooling can be higher in dark coats (Walsberg et al., 1978; Conley and Porter, 1986; Stahel et al., 1987; Walsberg and Wolf, 1995). So, under conditions of constant ambient temperature, black males may store more heat than blonde females if there is no wind. In the presence of strong wind, however, the same males can lose heat more easily than females. This may explain the apparent preference of adult males as resting partners by adult females during cold periods, as reported in this study and by C. Welker (personal communication, 1996) in captive black-and-gold howlers in Germany. Thus, by resting close to a more efficient heat-absorber black male during windy and cold periods, an adult female may gain more heat through convection and radiation.

No consistent differences were observed between age classes. It is possible that the

lower similarity between adults and subadults in terms of microhabitat selection/body regions exposed to sunlight may relate more to social than thermoregulatory factors. Subadult male and female howlers are reported to migrate from their natal groups (Calegario-Marques and Bicca-Marques, 1996).

#### Evolution of sexual dichromatism

Because this research failed to show intersexual differences in behavioral thermoregulation as should be expected by Thorington et al.'s (1979) model, black coloration of adult males in *A. caraya* is more likely related to sexual selection (see also Crockett, 1987). Sex differences in coat color in both other sexually dichromatic neotropical primate taxa (*A. f. clamitans* and *Pithecia pithecia chrysocephala*) are less than in *A. caraya* and similarly do not fit a thermoregulation model.

According to Darwin (1871), changes in coat color that occur during maturation and only in males support a model of sexual selection. Moreover, the evolution of particular traits through sexual selection might be expected in species in which individuals of one sex are characterized by high variance in reproductive success due to competition over mates (Darwin, 1871; Andersson, 1994). This is the case in *A. caraya*. Although individuals of both sexes tend to disperse near maturity (Rumiz, 1990; Calegario-Marques and Bicca-Marques, 1996), reproductive competition between males in black-and-gold howlers is much higher than in females. The number of breeding positions in a group for a female is greater than for a male (see Crockett and Eisenberg, 1987; Neville et al., 1988). Also, a single adult male can monopolize group females who come into estrus at different times throughout the year (Calegario-Marques and Bicca-Marques, 1993). Aggression between males has been reported in contexts of reproduction (Calegario-Marques and Bicca-Marques, 1997) and invasion of groups (Kowalewski et al., 1995). According to Crockett and Pope (1988), the ability to remain in a stable group through intrasexual aggression is essential for one's reproductive success in *Alouatta*.

Black-and-gold howlers live in social groups in which adult male takeovers are reported to be followed by infanticide (Rumiz, 1990; Zunino et al., 1986; Calegario-Marques and Bicca-Marques, 1996). Infanticide has also been reported in other howler species (Clarke, 1983; Crockett and Sekulic, 1984; Galetti et al., 1994) and hypothesized to be related to sexual selection (Kowalewski et al., 1995). This behavior has immediate negative results for the reproductive success of mothers. Consequently, female black-and-gold howlers seem to have little or no decision power in choosing a within-group mate. Emigrating females, however, may have more opportunities to choose, especially among solitary males (probably the losers of within-group male-male conflicts), because they have greater access to these males than do females living in established groups. Thus, it is more likely that black coat color in adult males evolved through intrasexual selection (see Halliday, 1994) due to male contest competition for access to mating partners, rather than through female choice (but see below and see Crockett, 1987). For example, a black coat might function to advertise resource occupancy, fighting ability, aggressiveness, health condition, or maturity and/or to help in sex recognition, as proposed for other sexually dichromatic animals (see Andersson, 1994). Although most of these possible color roles may influence both male-male competition and female choice, the observation of a delay in the onset of the beginning of color change in two black-and-gold juvenile male howlers (which looked like females) from a one-male group living in a forest fragment of 0.3 ha near the study site (Bicca-Marques, personal observation, 1989–1990) seems to support the intrasexual selection model. Due to its very reduced size, this fragment can only support a small howler group, and the chances of a juvenile male being evicted by the adult male may be greater here. Consequently, a color change delay may be an important mechanism allowing a juvenile male to reach a larger body size before being forced to emigrate if fur darkness functions as a stimulus driving the aggression of adult males toward maturing males in this species. The sexing of both juveniles as males in

the mentioned group was only made possible by observing their descended testes.

Black-and-gold male howlers also exhibit larger body size and hyoid volume than females (see Crockett and Eisenberg, 1987; Neville et al., 1988), differences probably evolved by intrasexual selection (Crockett, 1987). These traits, in conjunction with a social system characterized by a single dominant male, may serve an important function in home range and possibly mate defense. In *A. palliata*, on the other hand, hyoids are much smaller than in other howlers, and females are more similar to males in body size and hyoid volume (Crockett and Eisenberg, 1987). Unlike all other howler species, *A. palliata* lives in groups having more than one resident adult male and more than four adult females (see Crockett and Eisenberg, 1987; Smuts et al., 1987) in which male intrasexual agonistic interactions are rare (Clarke, 1986).

In New World monkeys, multimale-multi-female groups are found among atelines (*Ateles*, *Brachyteles*, and *Lagothrix*; see Smuts et al., 1987); in these groups, inter-male aggression is infrequent, and females actively choose mating partners (Robinson and Janson, 1987; Strier, 1990). This social organization is also present among *Cacajao*, *Chiropotes*, *Cebus*, and *Saimiri* (Robinson and Janson, 1987; Ayres, 1989). Thus, using a phylogenetic approach, the social organization of *A. palliata* seems to represent the primitive state for its genus, and the female choice hypothesis for the evolution of sexual dichromatism in *A. caraya* and *A. f. clamitans* receives some supportive evidence.

Nevertheless, why northern howler species (such as *A. seniculus* and *A. belzebul*) with similar social organizations did not evolve such dichromatism deserves future research. If the habitat of southern dichromatic howlers is found to have been more fragmented than that of northern nondichromatic howler species in the past, the appearance of distinctive males by chance mutations could have facilitated long-distance sex recognition by migrating individuals. This is a situation in which the female choice of distinctive males proposed by Crockett (1987) could advantageously operate. Actually, the current geographical distri-

bution of *A. caraya* is characterized by naturally occurring islands of forest interspersed by grasslands (see Bicca-Marques, 1990). Data on habitat structure during the radiation of the genus and the environmental conditions under which each species evolved are essential to clarify this issue.

Further explanations for this latitudinal difference are possible. For example, if adult female black-and-gold howlers that prefer resting in close proximity to adult males during cold periods have a higher survival and reproductive success, evolving darker males would form stronger consortships and have higher chances to mate with them. This is compatible with the observation that in *A. caraya* most births occur during the colder period of the year (Calegari-Marques and Bicca-Marques, 1993; Zunino, 1996). Although this scenario could satisfactorily explain the evolution of sexual dichromatism in *A. caraya* by female choice and the lack of such phenomenon in howler species inhabiting less thermally seasonal northern habitats, it does not appropriately account for the evolution of reddish males in *A. f. clamitans* living at similar latitudinal limits as *A. caraya*.

Female choice has also been proposed as the mechanism promoting the evolution of sexual dichromatism in *Eulemur macaco*, whose males are black and females are brown (Small, 1993). However, contrary to *A. caraya*, in this species the sexes are dichromatic at birth (Harrington, 1978). Due to the similarity in the pattern of sexual dichromatism in *A. caraya* and *E. macaco*, they might prove useful for evaluating models of sexual selection, coat color, and behavioral thermoregulation in other primate taxa. Data on the influence of male pelage coloration to female choice and male competitive skills, both affecting male fitness, shall provide some insight into these issues. Explanations using sexual selection and thermoregulation models, however, are not necessarily mutually exclusive. Even if future research identifies the existence of seasonal sexual advantages due to dichromatism, the evolution of this trait may still be better explained by some kind of sexual selection. Based on current data, however, it is not possible to determine which mechanism of sexual selection (female mate choice or male intrasexual

competition), if any, was the major factor responsible for the evolution of sexual dichromatism in *A. caraya*.

## CONCLUSIONS

Data presented in this study suggest that male and female black-and-gold howlers adopt behavioral strategies to regulate body temperature. The animals used energy-conserving postures, huddling, and the exposure to sunlight when resting under colder conditions. The opposite—energy-dissipating postures, increased interindividual distances, and shade-seeking—was observed mainly during periods of high ambient temperature.

Thermoregulatory behaviors seem to play an important role in the energy budget of black-and-gold howling monkeys. Energy conservation strategies may be essential, especially under conditions of climatic and/or food stress in more seasonal higher latitudes. Although it is currently difficult to completely reject the hypothesis that dichromatism in *A. caraya* evolved in response to different thermal requirements of males and females, our data indicate that males and females use thermoregulatory behaviors similarly. In the absence of support for a thermoregulatory role, we argue that a sexual selection hypothesis is more likely to account for color differences between male and female *A. caraya*. Future research should evaluate the effect of (1) wind speed, (2) humidity, (3) diet quality, and (4) other morphological and physiological traits on behavioral thermoregulation of black-and-gold howling monkeys, as well as evidence of color influence on male mating competition and female mate choice, to identify the evolutionary basis of sexual dichromatism.

## ACKNOWLEDGMENTS

The authors thank the Osório family for their permission to work on Estância Casa Branca and their support during the study, Dr. Steve Leigh for his help in the statistical analysis of the data, Dr. Paul Garber for helpful comments on earlier drafts of the manuscript, Dr. Emöke Szathmáry and three anonymous reviewers for invaluable suggestions, and the Universidade de Brasília and Universidade Federal do Rio Grande do Sul for logistical support. Júlio César Bicca-



Marques is currently supported by a doctoral studentship from the Brazilian Government/CAPES (1823/95-3) at the University of Illinois at Urbana-Champaign.

### LITERATURE CITED

- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227-265.
- Andersson M (1994) Sexual Selection. Princeton: Princeton University Press.
- Ayres JMC (1989) Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *J. Hum. Evol.* 18:697-716.
- Bicca-Marques JC (1990) A new southern limit for the distribution of *Alouatta caraya* in Rio Grande do Sul State, Brazil. *Primates* 31:449-451.
- Bicca-Marques JC (1991) Ecologia e Comportamento de um Grupo de Bugios-Pretos *Alouatta caraya* (Primates, Cebidae) em Alegrete, RS, Brasil. Master's thesis. Brasília, Brasil: Universidade de Brasília.
- Bicca-Marques JC (1993) Padrão de atividades diárias do bugio-preto *Alouatta caraya* (Primates, Cebidae): Uma análise temporal e bioenergética. In ME Yamamoto and MBC Sousa (eds.): *A Primatologia no Brasil-4*. Natal: Editora Universitária-UFRN, pp. 35-49.
- Bicca-Marques JC and Calegari-Marques C (1994a) Feeding behavior of the black howler monkey (*Alouatta caraya*) in a seminatural forest. *Acta Biol. Leopold* 16:69-84.
- Bicca-Marques JC and Calegari-Marques C (1994b) Activity budget and diet of *Alouatta caraya*: An age-sex analysis. *Folia Primatol.* 63:216-220.
- Bicca-Marques JC and Calegari-Marques C (1995) Locomotion of black howlers in a habitat with discontinuous canopy. *Folia Primatol.* 64:55-61.
- Brasil-IPAGRO (1989) Atlas Agroclimático do Estado do Rio Grande do Sul. Porto Alegre: Secretaria da Agricultura-RS.
- Calegari-Marques C and Bicca-Marques JC (1993) Reprodução de *Alouatta caraya* Humboldt, 1812 (Primates, Cebidae). In ME Yamamoto and MBC Sousa (eds.): *A Primatologia no Brasil-4*. Natal: Editora Universitária-UFRN, pp. 51-66.
- Calegari-Marques C and Bicca-Marques JC (1996) Emigration in a black howling monkey group. *Int. J. Primatol.* 17:229-237.
- Calegari-Marques C and Bicca-Marques JC (1997) Comportamento agressivo em um grupo de bugios-pretos, *Alouatta caraya* (Primates, Cebidae). In H Schneider, and SF Ferrari (eds.): *A Primatologia no Brasil-5*. Belém: Sociedade de Brasileira de Primatologia/Universidade Federal do Para, pp. 29-38.
- Canals M, Rosenmann M, and Bozinovic F (1989) Energetics and geometry of huddling in small mammals. *J. Theor. Biol.* 141:181-189.
- Casey TM (1981) Behavioral mechanisms of thermoregulation. In B Heinrich (ed.): *Insect Thermoregulation*. New York: John Wiley, pp. 79-114.
- Chivers DJ (1969) On the daily behaviour and spacing of howling monkey groups. *Folia Primatol.* 10:48-102.
- Clarke MR (1983) Infant killing and infant disappearance following male takeovers in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. *Am. J. Primatol.* 5:241-247.
- Clarke MR (1986) Interactions of adult male howling monkeys (*Alouatta palliata*) with immatures in a free-ranging social group. *Am. J. Phys. Anthropol.* 69:188.
- Conley KE, and Porter WP (1986) Heat loss from deer mice (*Peromyscus*): Evaluation of seasonal limits to thermoregulation. *J. Exp. Biol.* 126:249-269.
- Crockett CM (1987) Diet, dimorphism and demography: Perspectives from howlers to hominids. In WG Kinzey (ed.): *The Evolution of Human Behavior: Primate Models*. New York: SUNY Press, pp. 115-135.
- Crockett CM and Eisenberg JF (1987) Howlers: Variation in group size and demography. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.) *Primate Societies*. Chicago: The University of Chicago Press, pp. 54-68.
- Crockett CM and Pope T (1988) Inferring patterns of aggression from red howler monkey injuries. *Am. J. Primatol.* 5:289-308.
- Crockett CM and Sekulic R (1984) Infanticide in red howler monkeys (*Alouatta seniculus*). In G Hausfater, and SB Hrdy (eds.): *Infanticide—Comparative and Evolutionary Perspectives*. New York: Aldine, pp. 173-191.
- Dahl JF and Smith EO (1982) Thermoregulatory, microhabitat preferences of stump-tail macaques. *Am. J. Phys. Anthropol.* 57:179.
- Dahl JF, Bernstein IS, and Williams L (1982) Thermoregulation and social structure of a captive group of rhesus macaques. *Int. J. Primatol.* 3:273.
- Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex*. London: Murray.
- Dasilva GL (1993) Postural changes and behavioural thermoregulation in *Colobus polykomus*: The effect of climate and diet. *Afr. J. Ecol.* 31:226-241.
- Galetti M, Pedroni F, and Paschoal M (1994) Infanticide in the brown howler monkey, *Alouatta fusca*. *Neotrop. Primates* 2:6-7.
- Halliday TR (1994) Sex and evolution. In PJB Slater, and TR Halliday (eds): *Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 150-192.
- Harrington JE (1978) Development of behavior in *Lemur macaco* in the first nineteen weeks. *Folia Primatol.* 29:107-128.
- Heatwole H (1983) Physiological responses of animals to moisture and temperature. In FB Golley (ed.): *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier, pp. 239-278.
- Hill WCO (1962) *Primates: Comparative Anatomy and Taxonomy*, V, Cebidae, Part B. New York: Wiley Interscience.
- Hull D (1973) Thermoregulation in young animals. In GC Whittow (ed.): *Comparative Physiology of Thermoregulation*. New York: Academic Press, pp. 167-200.
- Jacobson AS and Nash LT (1995) Behavioral thermoregulation in a captive population of ring-tailed lemurs (*Lemur catta*). *Am. J. Primatol.* 36:130.
- Kowalewski M, Bravo SP, and Zunino GE (1995) Aggression between *Alouatta caraya* males in forest patches in Northern Argentina. *Neotrop. Primates* 3:179-181.
- Lapointe JF and Legendre P (1992) Statistical significance of the matrix correlation coefficient for comparing independent phylogenetic trees. *Syst. Biol.* 41:378-384.
- LeMaho Y, Goffart M, Rochas A, Felbabel H, and Chatonnet J (1981) Thermoregulation in the only nocturnal simian: The night monkey *Aotus trivirgatus*. *Am. J. Physiol.* 240:R156-R165.
- Malinow MR, Stahl WR, Maruffo CA, Pope BL, and Depaoli R (1966) Growth in howler monkeys. *Primates* 7:433-447.
- Milton K, Caset TM, and Casey KK (1979) The basal metabolism of mantled howler monkeys (*Alouatta palliata*). *J. Mammal* 60:373-376.
- Montgomery GG and Sunquist ME (1978) Habitat selection and use by two-toed and three-toed sloths. In GG Montgomery (ed): *The Ecology of Arboreal Folivores*. Washington, DC: Smithsonian Institution Press, pp. 329-359.
- Moreno JA (1961) *Clima do Rio Grande do Sul*. Porto Alegre: Secretaria da Agricultura.



- Morse DH (1980) Behavioral Mechanisms in Ecology. Cambridge: Harvard University Press.
- Neville MK, Glander KE, Braza F, and Rylands AB (1988) The howling monkeys, genus *Alouatta*. In RA Mittermeier, AB Rylands, AF Coimbra-Filho, and GAB Fonseca (eds.): Ecology and Behavior of Neotropical Primates. Vol. 2. Washington, DC: World Wildlife Fund, pp. 349–453.
- Oates JF (1977) The guereza and its food. In TH Clutton-Brock (ed.): Primate Ecology. London: Academic Press, pp. 276–321.
- Parker KL (1988) Effects of heat, cold, and rain on coastal black-tailed deer. Can. J. Zool. 66:2475–2483.
- Paterson JD (1980) A preliminary study of the relationships between ambient environment and positional thermoregulatory behavior in *Alouatta palliata*. Anthropol. Contemp. 3:254.
- Paterson JD (1981) Postural-positional thermoregulatory behaviour and ecological factors in primates. Can. Rev. Phys. Anthropol. 3:3–11.
- Paterson JD (1986) Shape as a factor in primate thermoregulation. In DM Taub, and FA King (eds.): Current Perspectives in Primate Social Dynamics. New York: Van Nostrand, pp. 228–242.
- Paterson JD (1994) Behavioral thermoregulation and structural adaptation in the Arashiyama "A" troop. In JR Anderson, JJ Roeder, B Thierry, and N Herrschmidt (eds.): Current Primatology. Vol. 3: Behavioural Neuroscience, Physiology and Reproduction. Strasbourg: Université Louis Pasteur, pp. 227–236.
- Pope BL (1966) The population characteristics of howler monkeys (*Alouatta caraya*) in northern Argentina. Am. J. Phys. Anthropol. 24:361–370.
- Prates JC, Kunz Jr LF, Rosa AO, Assis-Jardim MM, and Canto-Silva CR (1993) Primatas do Rio Grande do Sul: Ocorrência em unidades de conservação. In ME Yamamoto, and MBC Sousa (eds.): A Primatologia no Brasil-4. Natal: Editora Universitária-UFRN, pp. 183–194.
- Prost JH (1965) A definitional system for the classification of primate locomotion. Am. Anthropol. 67:1198–1214.
- Robinson JG and Janson CH (1987) Capuchins, squirrel monkeys, and atelines: Socioecological convergence with Old World primates. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, TT Struhsaker (eds.): Primate Societies. Chicago: The University of Chicago Press, pp. 69–82.
- Rohlf FJ (1994) NTSYS-pc: Numerical Taxonomy and Multivariate Analysis System. Version 1.80. New York: Applied Biostatistics Inc.
- Rosenberger AL and Strier KB (1989) Adaptive radiation of the ateline primates. J. Hum. Evol. 18:717–750.
- Roverud RC and Chappell MA (1991) Energetic and thermoregulatory aspects of clustering behavior in the neotropical bat *Noctilio albiventris*. Physiol. Zool. 64:1527–1541.
- Rowe N (1996) The Pictorial Guide to the Living Primates. East Hampton: Pogonias Press.
- Rumiz DI (1985) Ecología poblacional de *Alouatta caraya* en el norte de Argentina. Ph.D. dissertation. Buenos Aires: Facultad de Ciencias Naturales y Museo.
- Rumiz DI (1990) *Alouatta caraya*: Population density and demography in northern Argentina. Am. J. Primatol. 21:279–294.
- Santini MEL (1985) Alimentação e padrões de atividade de *Alouatta caraya* (Primates, Cebidae) reintroduzido no Parque Nacional de Brasília, DF. Master's thesis. Brasília, Brasil: Universidade de Brasília.
- Schmidt-Nielsen K (1990) Animal Physiology: Adaptation and Environment. 4th ed., Cambridge: Cambridge University Press.
- Small MF (1993) Female Choices: Sexual Behavior of Female Primates. Ithaca: Cornell University Press.
- Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, and Struhsaker TT (1987) The order primates: Species names and a guide to social organization. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.): Primate Societies. Chicago: The University of Chicago Press, pp. 499–505.
- Stahel CD, Nicol SC, and Walker GJ (1987) Heat production and thermal resistance in the little penguin *Eudyptula minor* in relation to wind speed. Physiol. Zool. 60:413–423.
- Stapp P, Pekins PJ, and Mautz WW (1991) Winter energy expenditure and the distribution of southern flying squirrels. Can. J. Zool. 69:2548–2555.
- Stelzner JK and Hausfater G (1986) Posture, microclimate and thermoregulation in yellow baboons. Primates 27:449–463.
- Strier KB (1990) New World primates, new frontiers: Insights from the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). Int. J. Primatol. 11:7–19.
- Thorington RW Jr, Rudran R, and Mack D (1979) Sexual dimorphism in *Alouatta seniculus* and observations on capture techniques. In JF Eisenberg (ed.): Vertebrate Ecology in the Northern Neotropics. Washington, DC: Smithsonian Institution Press, pp. 97–106.
- Thorington RW Jr, Ruiz JC, and Eisenberg JF (1984) A study of a black howler monkey (*Alouatta caraya*) population in northern Argentina. Am. J. Primatol. 6:357–366.
- Velleman PF and Hoaglin DC (1981) Applications, Basics, and Computing of Exploratory Data Analysis. Boston: Duxbury.
- Walsberg GE (1983) Coat color and solar heat gain in animals. Bioscience 33:88–91.
- Walsberg GE (1988a) The significance of fur structure for solar heat gain in the rock squirrel, *Spermophilus variegatus*. J. Exp. Biol. 138:243–257.
- Walsberg GE (1988b) Consequences of skin color and fur properties for solar heat gain and ultraviolet irradiance in two mammals. J. Comp. Physiol. 158B:213–221.
- Walsberg GE and Schmidt CA (1989) Seasonal adjustment of solar heat gain in a desert mammal by altering coat properties independently of surface coloration. J. Exp. Biol. 142:387–400.
- Walsberg GE and Wolf BO (1995) Effects of solar radiation and wind speed on metabolic heat production by two mammals with contrasting coat colours. J. Exp. Biol. 198:1499–1507.
- Walsberg GE, Campbell GS, and King JR (1978) Animal coat color and radiative heat gain: A re-evaluation. J. Comp. Physiol. 126B:211–222.
- Walter H (1971) Ecology of Tropical and Subtropical Vegetation. Edinburgh: Oliver and Boyd.
- Wilkinson LE (1990) SYSTAT. Evanston: Systat Inc.
- Yahav S and Buffenstein R (1991) Huddling behavior facilitates homeothermy in the naked mole rat *Heterocephalus glaber*. Physiol. Zool. 64:871–884.
- Young OP (1982) Aggressive interaction between howler monkeys and turkey vultures: The need to thermoregulate behaviorally. Biotropica 14:228–231.
- Zunino GE (1986) Algunos Aspectos de la Ecología y Etología del Mono Aullador Negro (*Alouatta caraya*) en Habitats Fragmentados. Ph.D. thesis. Buenos Aires, Argentina: Universidad de Buenos Aires.
- Zunino GE (1996) Análisis de nacimientos en *Alouatta caraya* (Primates, Cebidae), en el noreste de la Argentina. Rev. Mus. Arg. Cien. Nat. "Bernardino Rivadavia." Nueva Serie 133:1–10.
- Zunino GE, Chalukian SC, and Rumiz DI (1986) Infanticidio y desaparición de infantes asociados al reemplazo de machos en grupos de *Alouatta caraya*. In MT Mello (ed.): A Primatologia no Brasil-2. Brasília: Sociedade Brasileira de Primatologia, pp. 185–190.